WINGBEAT FREQUENCY AND THE BODY DRAG ANOMALY: WIND-TUNNEL OBSERVATIONS ON A THRUSH NIGHTINGALE (*LUSCINIA LUSCINIA*) AND A TEAL (*ANAS CRECCA*)

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Summary

A teal (*Anas crecca*) and a thrush nightingale (*Luscinia luscinia*) were trained to fly in the Lund wind tunnel for periods of up to 3 and 16 h respectively. Both birds flew in steady flapping flight, with such regularity that their wingbeat frequencies could be determined by viewing them through a shutter stroboscope. When flying at a constant air speed, the teal's wingbeat frequency varied with the 0.364 power of the body mass and the thrush nightingale's varied with the 0.430 power. Both exponents differed from zero, but neither differed from the predicted value (0.5) at the 1 % level of significance. The teal continued to flap steadily as the tunnel tilt angle was varied from −1 ° (climb) to +6 ° (descent), while the wingbeat frequency declined progressively by about 11 %. In both birds, the plot of wingbeat frequency against air speed in level flight was U-shaped, with small but statistically significant curvature. We identified the minima of these curves with the minimum power speed (V_{mp}) and found that the values predicted for V_{mp}, using previously published default values for the required variables, were only about two-thirds of the observed minimum-frequency speeds. The discrepancy could be resolved if the body drag coefficients (C_{Db}) of both birds were near 0.08, rather than near 0.40 as previously assumed. The previously published high values for body drag coefficients were derived from wind-tunnel measurements on frozen bird bodies, from which the wings had been removed, and had long been regarded as anomalous, as values below 0.01 are given in the engineering literature for streamlined bodies. We suggest that birds of any size that have well-streamlined bodies can achieve minimum body drag coefficients of around 0.05 if the feet can be fully retracted under the flank feathers. In such birds, field observations of flight speeds may need to be reinterpreted in the light of higher estimates of V_{mp}. Estimates of the effective lift:drag ratio and range can also be revised upwards. Birds that have large feet or trailing legs may have higher body drag coefficients. The original estimates of around $C_{Db}=0.4$ could be correct for species, such as pelicans and large herons, that also have prominent heads. We see no evidence for any progressive reduction of body drag coefficient in the Reynolds number range covered by our experiments, that is 21 600–215 000 on the basis of body cross-sectional diameter.

Introduction

According to Pennycuick (1996) the wingbeat frequencies (*f*) of different birds, when all are in level cruising flight, are given by:

$$f = (m\boldsymbol{g})^{1/2}b^{-17/24}S^{-1/3}I^{-1/8}\rho^{-3/8}, \tag{1}$$

where *m* is the body mass, $\boldsymbol{g}$ is the acceleration due to gravity, *b* is the wing span, *S* is the wing area, *I* is the wing moment of inertia and ρ is the air density. The five exponents in equation 1 are related to each other by three equations, which express the condition that the expression on the right-hand side must have the correct dimensions (inverse time). These equations were derived by Pennycuick (1990), who selected a set of values for the exponents that satisfied the dimensional constraints and also fitted data from 32 species, whose wingbeat frequencies had been observed in the field. The original set of exponents was changed slightly by Pennycuick (1996), to make equation 1 give a better fit to an enlarged data set, incorporating 15 additional species. Any set of exponents that satisfies the dimensional constraints gives an allometric relationship for geometrically similar birds, whereby the wingbeat frequency varies with the −1/6 power of the body mass.

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The empirical observations referred to differences in wingbeat frequency between species, where all were assumed to be flying under the same conditions, defined as level flight at a fixed multiple of the minimum power speed. The body measurements used were means of samples of different species. However, equation 1 was derived from a dimensional argument, and it can therefore be used in a very different way, to predict the effect on an individual bird's wingbeat frequency if the body mass or the air density were to vary while the wing span, wing area and wing moment of inertia remain constant. Equation 1 predicts that if the body mass or air density were to change in the course of a flight, this should cause the wingbeat frequency to change in proportion to the square root of the mass and the −3/8 power of the air density. These predictions can only be checked by experiments on individual birds, not from inter-species comparisons based on field data.

We have observed the wingbeat frequencies of two birds of different species that were trained to fly for prolonged periods in a wind tunnel. We have not yet been able to test the effect of changes in air density, but we have observed the effects of changes in body mass and of two additional variables not considered in the earlier analysis, air speed and angle of climb or descent.

Materials and methods

Wind tunnel

Our experiments were conducted in a large, low-turbulence wind tunnel at Lund University, Sweden. C. J. Pennycuick, T. Alerstam and A. Hedenström (in preparation) describe the wind tunnel and explain its design, which represents a radical departure from earlier wind tunnels used for bird flight research. The wind speed, which is also the bird's air speed, can be precisely controlled and continuously monitored. The whole wind tunnel can be tilted, so as to impose either level flight or a known angle of climb or descent. The test section is octagonal, 1.20 m wide by 1.08 m high. The first 1.2 m of its length is enclosed by Plexiglas walls, after which there is an open section 0.5 m long. A preliminary pitot-static survey at 119 points across the test section showed that the variation was within ±1.3 % of the mean speed, except for three points in the extreme corners, with speed deficits of up to 7 % of the mean speed.

Equivalent air speed

We set and monitored the dynamic pressure (q), rather than the air speed as such, but we expressed it in the form of the 'equivalent air speed' (V_e), defined as:

$$V_e = \sqrt{(2q/\rho_0)}, \qquad (2)$$

where ρ_0 is a fixed value of the air density (1.23 kg m^{-3}) assigned to sea level in the International Standard Atmosphere. If the actual air density is equal to ρ_0, then the equivalent air speed is the same as the 'true air speed', which is the speed at which a light particle is carried along in the air. Usually the true and equivalent air speeds are not identical, and the disparity between them varies from day to day because of changes in air temperature and barometric pressure. In that case, we prefer to set and monitor the equivalent, rather than the true, air speed. This is because the equivalent air speed determines the magnitudes of the aerodynamic forces acting on the bird, and because the bird's minimum power speed is more nearly constant in terms of equivalent than of true air speed.

Birds and training

Two birds were used, a thrush nightingale (*Luscinia luscinia* Linnaeus) and a teal (*Anas crecca* Linnaeus). The methods of training were determined by the requirements of physiological experiments, and the details will be given in a later publication with the results of those experiments. Both birds were trained primarily to fly horizontally for prolonged periods, the nightingale for up to 16 h and the teal for up to 3 h, with short interruptions for the bird to be taken out and weighed. A nylon fishing net, made of a square 17 mm×17 mm mesh of brown nylon thread 0.75 mm in diameter, was stretched across the upstream end of the test section during experiments with the teal so as to prevent it from flying into the contraction, but this was not needed when flying the thrush nightingale. Preliminary tests using a hot-wire anemometer showed that the root mean square (RMS) value of longitudinal turbulence was 1.2 % of the mean speed with the net installed. Without the net, the turbulence level was too low for consistent measurements with the equipment available.

Measurement of wingbeat frequency

Wingbeat frequency was measured using a shutter (mechanical) stroboscope. This consisted of a black plastic cylinder 31 mm in diameter (actually a 35 mm film can) mounted on the spindle of a stepper motor giving 48 steps per revolution. The cylinder had four holes spaced equally around its circumference and was mounted inside a black box with minimal clearance. Holes in the opposite walls of the box allowed the bird to be viewed through the holes in the cylinder, when these were aligned with the holes in the box. The stepper motor was driven by a chip designed for that purpose (SAA1027) and this, in turn, was fed by a pulse train supplied by a combined oscillator and divider chip (μA2240CN). The combined effect of dividing the oscillator frequency by 128, then by the 48 steps of the stepper motor, and finally multiplying by four for the four holes in the cylinder, was that the oscillator frequency was 1536 times the shutter frequency. To measure the wingbeat frequency, the oscillator was adjusted until the wings appeared to be stationary. This was only possible when the bird was flapping steadily and remained in a steady position in the test section for several seconds. The oscillator frequency, which was in the range 12–20 kHz for our observations, was read to four-digit precision from a multimeter (Precision Gold M810) and divided by 1536 to obtain the wingbeat frequency. Some additional wingbeat frequencies for the teal were obtained from video recordings (at 25 frames s^{-1}), taken with a Panasonic NV-MS1 S-VHS camcorder, by counting the number of frames for 50 wingbeat cycles.

Results

Flight behaviour

After some weeks of initial training, both the thrush nightingale and the teal would fly for hours in steady flapping flight. The wingbeat in the teal was so regular that, if the shutter stroboscope was set slightly above or below the wingbeat frequency, the wings could be viewed apparently moving slowly and steadily up and down for prolonged periods. The thrush nightingale showed similarly regular flapping on some flights, but often there were momentary checks in the wingbeat cycle, which were seen as sudden jumps in the apparent wing position when viewed through the stroboscope. These checks were too brief for naked-eye observation, but high-speed video showed that the wings were held in the horizontal position for a fraction of a wingbeat period. The thrush nightingale never closed its wings during flight and did not exhibit any behaviour approaching the 'bounding' style of intermittent flight, often seen in small passerines. At the time of these observations, our training methods had not been developed to the point where the bird's position in the test section could be closely controlled. Both birds were observed when flying in the closed part of the test section, above the midline, but not very close to the upper walls. Both remained in this part of the tunnel for prolonged periods, with occasional excursions to the lower part of the test section or downstream to the open part. As noted above, it was only possible to measure the wingbeat frequency when the bird was holding a steady position in the test section. Beyond the lower and upper extremes of the usable speed range, the birds either refused to fly or flew in an unsteady way. For example, the highest speed at which we observed wingbeat frequencies in the thrush nightingale was $11.0 \, \mathrm{m \, s^{-1}}$, but we did not use these data, because the bird's speed did not match the wind speed, as it cyclically moved upwind and then drifted back downwind. Such behaviour was not seen in the teal at any speed, or in the thrush nightingale at lower speeds.

Effect of body mass on wingbeat frequency

Fig. 1 is a double-logarithmic plot showing 16 samples of wingbeat frequency measurements, taken during a single 16 h flight of the thrush nightingale on 21 September 1995. Each sample consisted of five observations of wingbeat frequency, each taken within 2–5 min with the shutter stroboscope, at 45 min past each hour, desynchronising the stroboscope after each observation, then resetting it to the wingbeat frequency. Both birds were capable of altering their wingbeat frequencies on a much shorter time scale than the minimum 30 s interval between measurements, so that each observation was fully independent of those before and after it. The bird was weighed once per 4 h (five times in all) at 20 min past the hour. The body mass was assumed to be constant within each sample of five wingbeat frequency observations and was estimated by linear interpolation between weighings. It declined from 27.49 g at the first sample to 22.19 g at the last, that is by 19 %
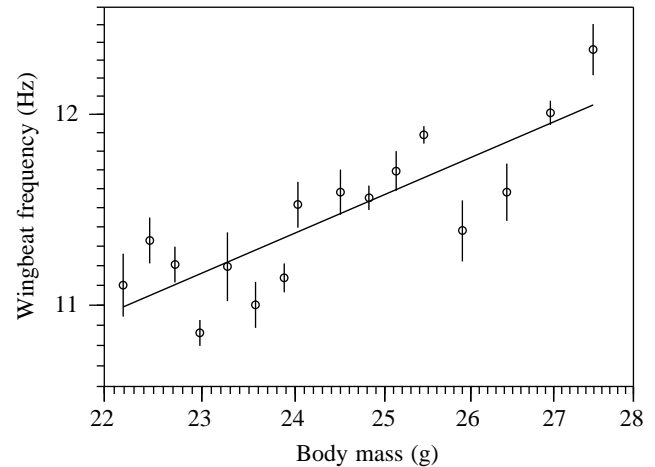

Fig. 1. Double-logarithmic plot of wingbeat frequency, observed at 1 h intervals during 16 h of horizontal flight at an equivalent air speed of $10.0 \, \mathrm{m \, s^{-1}}$ by the thrush nightingale *versus* interpolated body mass. Each of the 16 samples consisted of five observations taken within 2–5 min. Vertical bars show standard error (S.E.M.) above and below mean frequency. The slope of the linear regression line is 0.430 ± 0.0765, $r=0.832$.

of the starting mass. The equivalent air speed was held constant at $10.0 \, \mathrm{m \, s^{-1}}$, the speed to which the bird had become accustomed during training. The air density was $1.20 \, \mathrm{kg \, m^{-3}}$ at the beginning of the flight and $1.19 \, \mathrm{kg \, m^{-3}}$ at the end. Fig. 2 is a similar plot showing 30 measurements of wingbeat frequency in the teal (not grouped into samples), from video recordings taken during training flights on 6 days between 25 November and 3 December 1995, in the course of which the mass varied between 219.5 and 243.5 g. The equivalent air speed was $13.1 \, \mathrm{m \, s^{-1}}$, as used during training. The slopes of the linear regression lines from the double-logarithmic plots of Figs 1 and 2 are 0.430 and 0.364 respectively. Both slopes differ from zero at the 1 % level of significance (Table 1), confirming our surmise that individual birds, at least for these two species, do indeed adjust their wingbeat frequencies in response to changes in their body mass. The slope for the teal is significantly less than our expected value of 0.5 at the 5 % level, but neither slope differs significantly from 0.5 at the 1 % level. The marginally significant difference of the slope below 0.5 in the teal could be an artefact caused by the limited range

Table 1. *Slopes of the linear regressions of log-transformed values from Figs 1 and 2 compared using* t-*tests with hypothetical exponents of zero (null hypothesis) and 0.5 (expected value)*

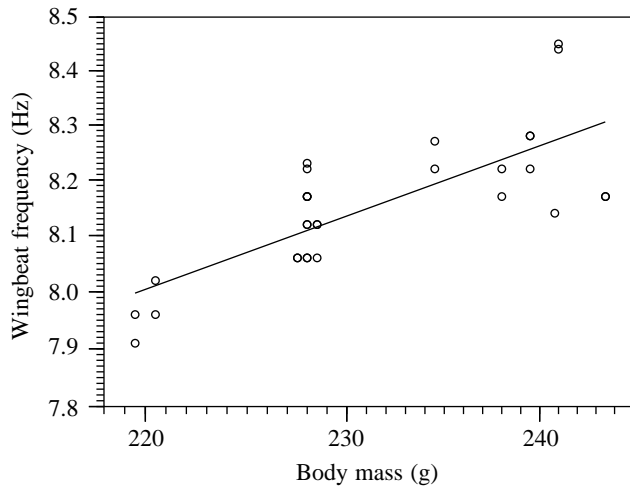| Bird	Slope	S.E.M.	d.f.	Test slope	*t*	*P*
Teal	0.364	0.0587	28	0.5	2.31	>0.02
				0	6.17	≪0.01
Thrush nightingale	0.430	0.0765	14	0.5	0.915	>0.05
				0	5.62	≪0.01

Fig. 2. Double-logarithmic plot of wingbeat frequency during six horizontal flights at an equivalent air speed of 13.1 m s^{-1} by the teal *versus* body mass. The slope of the linear regression line is 0.364±0.0587 (S.E.M.), *r*=0.761, *N*=30.

over which the mass varied, the lowest mass being only 9.9 % below the highest. According to Snedecor (1946), the effect of uncertainties in measuring the independent variable is to bias the slope of the linear regression downwards, and the effect is accentuated if the range of variation of this variable is small.

Effect of climb or descent on wingbeat frequency

Fig. 3 shows a linear plot of 110 observations of wingbeat frequency, obtained during a single flight of the teal, during which the wind tunnel was tilted to various angles between +6 ° (bird descending) and −1 ° (climbing). We initiated this experiment in level flight, at an equivalent air speed of 13.7 m s^{-1}, intending to maintain this speed throughout. On
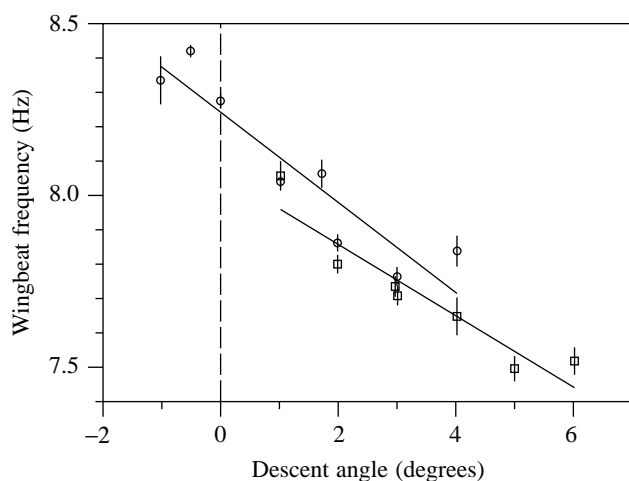

Fig. 3. Linear plot of wingbeat frequency during a single flight of the teal, *versus* wind tunnel tilt angle. Each point is the mean ± S.E.M. of a sample of at least six observations. Circles, 13.7 m s^{-1} (*N*=58); squares, 15.8 m s^{-1} (*N*=52).

reaching 4 ° descent, we expected the teal to glide, but it made no attempt to do this and continued flapping steadily as usual. At steeper angles, it could not maintain its position in the test section and was only restrained by the net from flying into the contraction. When we increased the speed to 15.8 m s^{-1}, the teal was able to descend at 6 °, still flapping steadily. It was able to maintain 15.8 m s^{-1} as we reduced the descent angle to 1 °, but it could not fly horizontally at this speed. When we reduced the speed back to 13.7 m s^{-1}, it was able to fly level and also to climb at 1 °. The data at the two speeds have been plotted separately in Fig. 3, with separate linear regression lines. This flight lasted 95 min, during which the mass decreased from 240 to 230 g.

Changing the angle of descent had a strong effect on the wingbeat frequency, with no change in the style of flight that would have been apparent in the field. The teal did not glide, flap intermittently, lower its feet or show any obvious changes of behaviour associated with the changing descent angle. This effect could be a significant source of error in field observations of wingbeat frequency, as it is usually difficult to be sure that a bird is flying horizontally unless it is flying low over a smooth water surface and, in that case, it may be gaining some advantage from ground effect. The effect of imposing an angle of descent on the bird is to reduce the mechanical power output required from its flight muscles, and Fig. 3 shows that this was accompanied by a reduction in wingbeat frequency, but not a proportional reduction. The steepest angle that we used, 6 °, corresponds to a glide ratio of 9.6 and should be steep enough to allow the teal to glide. At this angle of descent, the teal would have been exerting a mean thrust force near zero and possibly negative. It did not glide, and only reduced its wingbeat frequency by approximately 10 % below its value in level flight, while the mechanical power required had been reduced to zero, and possibly below. Fig. 3 therefore shows that the wingbeat frequency cannot be used as a proportional measure of mechanical power output, but that it did progressively follow changes of power output over a wide range. We used this result to interpret the next experiment.

Effect of air speed on wingbeat frequency

Fig. 4 is a linear plot of 88 observations of wingbeat frequency obtained during three flights of the teal, between 28 November and 4 December 1995. The flight durations were 44, 96 and 131 min, and the mass losses were 5.3, 8.8 and 12.3 g, respectively, from starting masses of between 236 and 246 g. The air flow was horizontal throughout these flights, and the equivalent air speed was varied between 10 and 16 m s^{-1}. The points for each flight show a U-shaped distribution. Each curve shown in the figure is a least-squares fit of the equation:

$$f = a + b/V + cV^3, \tag{3}$$

where *f* is the wingbeat frequency, *V* is the air speed and *a*, *b* and *c* are constants. This is the form of the curve of mechanical power *versus* speed used by Pennycuick (1975, 1989) for speeds in the vicinity of the minimum power speed. The

equivalent air speeds at the minima of the fitted curves were almost the same: $12.5\,\mathrm{m\,s^{-1}}$ for the first and second flights and $12.3\,\mathrm{m\,s^{-1}}$ for the third. The filled circle at the extreme top left of Fig. 4 represents two observations of wingbeat frequency at 8.67 and 8.68 Hz, which were obtained just after we set the equivalent air speed to $10.0\,\mathrm{m\,s^{-1}}$ during the third flight. The teal flew for a few seconds at this speed, close to the net at the upstream end of the test section, and then refused to fly. When we increased the speed to $10.3\,\mathrm{m\,s^{-1}}$, it flew normally with the wingbeat frequencies marked by crosses. The curve was fitted through the points marked by the crosses, not including the filled circle at $10.0\,\mathrm{m\,s^{-1}}$. The teal appeared to be most comfortable at equivalent air speeds between 12.0 and $13.5\,\mathrm{m\,s^{-1}}$. It would only fly for short periods, if at all, at speeds above 15 and below $10\,\mathrm{m\,s^{-1}}$.

The curved lines of Fig. 4 fit their respective sets of points significantly better than linear regression lines. This was tested by the variance ratio test (*F*-test) of Snedecor (1946), in which the mean square of deviations from the curved line was compared with that from the linear regression line. The variance ratios were highly significant at the 1 % level for all three flights, showing that the minima of the curves of Fig. 4 may be used to identify a meaningful 'minimum frequency speed'. The data from the three flights of the teal have been combined into a single curve in Fig. 5, in which the data are shown as means of observations at each value of the air speed. The variance ratio for curvature of this line according to equation 3 is $F=26.9$ for 1 and 15 degrees of freedom. For the thrush nightingale curve, which combines the data from two flights, $F=4.96$ for 1 and 11 degrees of freedom. Curvature is significant in both cases ($P<0.01$). The curvature is seen to be slight when plotted with a frequency scale extending down to zero, as in Fig. 5, although it is readily apparent to the eye on the expanded vertical scale of Fig. 4.
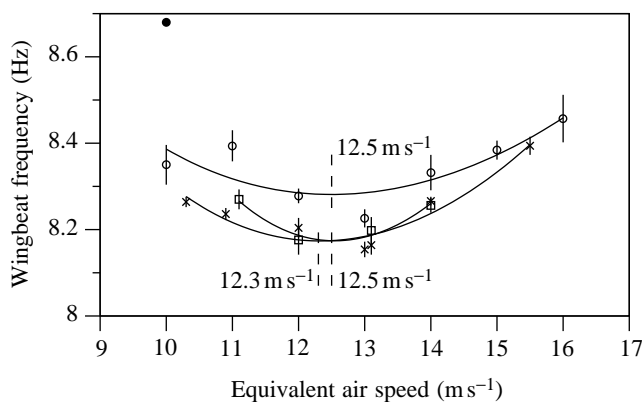

Fig. 4. Linear plot of wingbeat frequency (*f*) during three flights of the teal in horizontal flight *versus* equivalent air speed (*V*). Open circles are fitted by $f=6.67+15.1/V+0.000206V^3$ (*N*=33). Squares are fitted by $f=3.76+41.6/V+0.000559V^3$ (*N*=20). Crosses are fitted by $f=5.78+22.0/V+0.000317V^3$ (*N*=35). Minimum frequency speeds from these formulae are shown for each curve. Each point and bar shows mean frequency ± S.E.M. for a sample of observations at one speed. See text for explanation of filled circle at upper left.
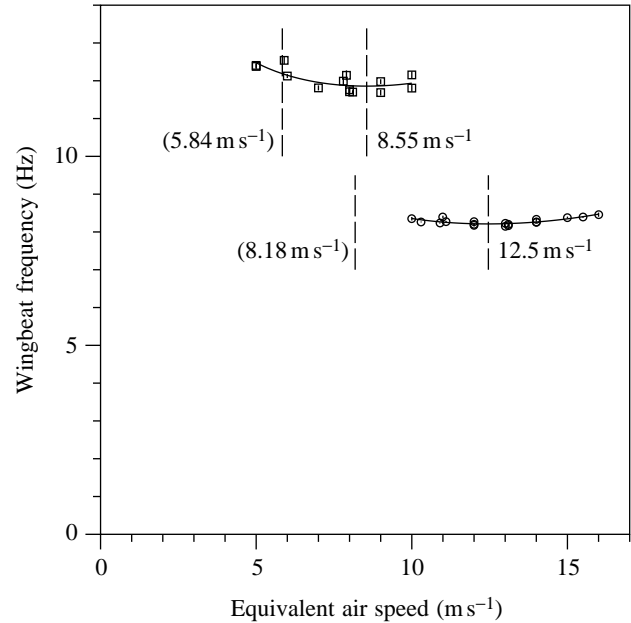

Fig. 5. Linear plot of wingbeat frequency *versus* equivalent air speed in horizontal flight. Combined data for two flights of the thrush nightingale (squares) and three flights of the teal (circles). Standard error bars are shown, but are mostly smaller than the symbols marking the means of samples when the data are plotted on this unexpanded scale. The minimum of each fitted curve is marked. The minimum power speed, estimated with data from Table 2 and using default values of variables from Program 1A of Pennycuick (1989), is given in parentheses for each bird.

Discussion

Discrepancy in the minimum power speed

We regard the minimum frequency speed as an experimental estimate of the minimum power speed V_{mp}. The basis for this assumption is the result shown in Fig. 3, which indicates that the wingbeat frequency varies progressively in the same direction as the power required from the muscles. An observed minimum in the curve of frequency *versus* speed should therefore correspond to a minimum in the curve of power required *versus* speed. The variation in wingbeat frequency at different speeds was small and no doubt proportionally much smaller than the variation in power required.

According to Pennycuick (1975), the minimum power speed for a bird in level flight (V_{mp}) can be calculated from the formula:

$$V_{\mathrm{mp}} = \frac{0.807(m\boldsymbol{g})^{1/2}k^{1/4}}{\rho^{1/2}b^{1/2}(S_{\mathrm{b}}C_{\mathrm{Db}})^{1/4}}, \qquad (4)$$

where m is the body mass, $\boldsymbol{g}$ is the acceleration due to gravity, ρ is the air density, b is the wing span, k is the induced drag factor, S_{b} is the frontal cross-sectional area of the body and C_{Db} is the drag coefficient of the body. The underlying assumption is that the curve of power *versus* speed must pass through a minimum, because it represents the sum of the induced power (P_{ind}), required to support the weight, and the parasite power

Table 2. *Values of variables used in calculating* V*mp* *from equation 4*

Variable	Symbol	Thrush nightingale	Teal
Body mass (kg)	m	0.027	0.235
Wing span (m)	b	0.263	0.582
Wing area (m²)	S	0.0130	0.0458
Body frontal area (m²)	S_b	0.000733	0.00310
Body drag coefficient	C_{Db}	0.40	0.381
Induced drag factor	k	1.2	
Gravity (m s⁻²)	g	9.81	
Air density (kg m⁻³)	ρ	1.23	

(P_{par}), required to overcome the drag of the body. Through the middle range of speeds, P_{ind} declines with increasing speed, but P_{par} increases, so that the curve of the sum of the two components is U-shaped. The speed (V_{mp}) at which the minimum occurs depends on the relative magnitudes of the induced and parasite powers. More induced power and/or less parasite power shift V_{mp} to a higher value. Estimates for V_{mp} for the teal and the thrush nightingale, calculated from equation 4 using the values for the variables given in Table 2, including default values from Pennycuick (1989) for k and C_{Db}, are shown in parentheses in Fig. 5. If we are correct in identifying the minimum frequency speed as an experimental estimate of V_{mp}, as argued above, then Fig. 5 shows a major discrepancy between observed and estimated values, which is in the same direction and of much the same magnitude in both of these very different species. While we cannot give fiducial limits for our minimum frequency speeds, we noted that the teal would not fly at its calculated minimum power speed, while the thrush nightingale did so reluctantly, with its body tilted in a pronounced nose-up attitude. A similar discrepancy was noted by Rothe and Nachtigall (1987), who reported that the minimum rate of oxygen consumption in pigeons flying in a wind tunnel occurred at a speed well above the calculated minimum power speed and that their pigeons were reluctant or unable to fly at the calculated value for V_{mp}.

Possible sources of discrepancy

The theory behind equation 4 is based on straightforward physical principles, derived from aeronautical engineering. Although the calculation of induced power, in particular, is much simplified from the reality of the flapping wings, there has been no suggestion that this is likely to cause a massive underestimate of induced power at medium speeds, as would be required to account for the observed discrepancy. It has also been assumed, perhaps wrongly, that any further components of power are independent of speed in this speed range. In particular, profile power (P_{pro}), which is needed to overcome the profile drag of the wings, has never been directly measured, and very little is known about it. If it were to decline strongly with speed in the vicinity of V_{mp}, this would shift the minimum power speed to a higher value. Actually, some early calculated curves of P_{pro} did show such a characteristic (Pennycuick, 1968b), but the

calculation involved many assumptions and the effect was, in any case, far too weak to account for our present discrepancy. The assumption that P_{pro} is independent of speed is currently the best approximation that can be reconciled with the available evidence about its behaviour at medium speeds (Pennycuick, 1995). An error in the relative magnitudes of P_{ind} and P_{par} is most likely to be the source of the discrepancy seen in Fig. 5.

If a structural error in the theory seems unlikely to account for the discrepancy, then we have to consider whether it could be due to a gross error in one or more of the values that we assigned to the seven variables on the right-hand side of equation 4 (Table 2). This also seems unlikely in the case of m, b and ρ, which were measured, while the acceleration due to gravity (g) was assigned a standard value, which is not likely to be far out. The body cross-sectional area S_b was calculated from m using the formula:

$$S_b = 0.00813 m^{0.666}, \qquad (5)$$

which was derived empirically from measurements on raptors and waterfowl by Pennycuick *et al.* (1988). As V_{mp} depends only weakly on S_b (it is proportional to S_b to the −0.25 power), it is unlikely that errors in estimating S_b could be large enough to cause the observed discrepancy.

This narrows the probable source of the discrepancy to the two dimensionless numbers C_{Db} and k which, respectively, express the degree of streamlining of the body and the degree of inefficiency with which the flapping wings generate lift. The body drag coefficient (C_{Db}) was assigned values according to a formula proposed by Pennycuick *et al.* (1988) and incorporated in the computer programs of Pennycuick (1989). This formula was empirically based on wind-tunnel measurements of the drag of frozen bird bodies, whose wings had been removed, and takes account of the likely Reynolds number, assigning drag coefficients ranging from 0.40 for small birds to 0.25 for large ones. The induced drag factor k was assigned a fixed value (k=1.2), which is essentially a guess based on aeronautical experience.

Fig. 6 shows the effect of changing our assumptions about the values of k and C_{Db} in the form of a family of curves for each bird, in which the estimated V_{mp} from equation 4 is plotted against C_{Db} for different values of k, retaining the values in Table 2 for the remaining five variables. The filled circles at the bottom right of each plot represent the default values listed in Table 2. The values of k for the four curves in each family range from 1.0 to 2.2. A value of k=1.0 represents an 'ideal' pair of wings, which generate force with no waste of energy, whereas k=2.2 represents a level of inefficiency which would be considered unacceptable in any flying machine and which, if found in an animal, would be quickly disposed of by natural selection. Moving each of the filled circles upwards, even as far as the curve for k=2.2, would increase the estimate of V_{mp}, but not nearly enough to account for the discrepancies seen in Fig. 5. While our default value for k is not experimentally based, we would have to increase it by an unbelievable amount in order to resolve the discrepancy in V_{mp}. However, a drastic reduction of C_{Db} by a factor of about
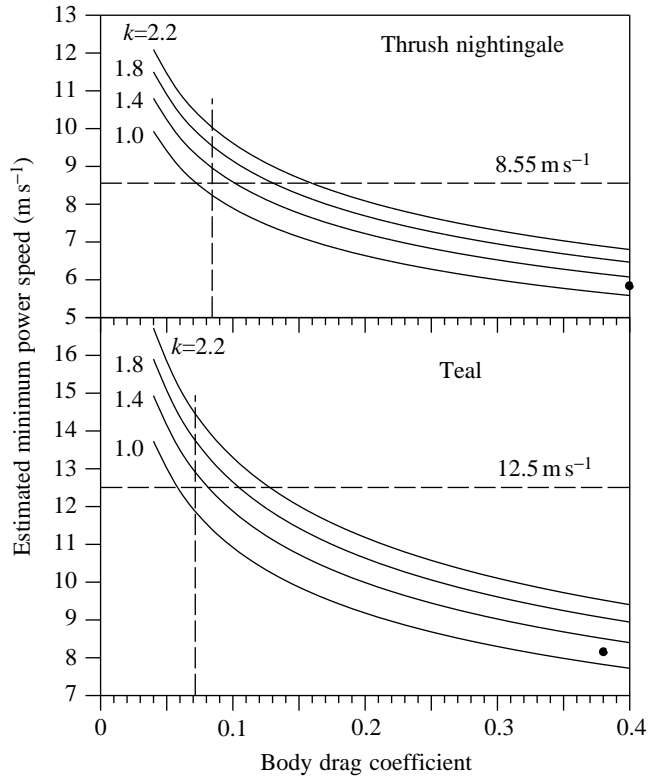
Fig. 6. Effect on the predicted minimum power speed of varying the assumed values of the induced power factor (*k*) and the body drag coefficient, for the thrush nightingale and the teal. Filled circles at bottom right show default values used in Program 1A of Pennycuick (1989), and broken lines show estimates derived from wingbeat frequency curves (Fig. 5).
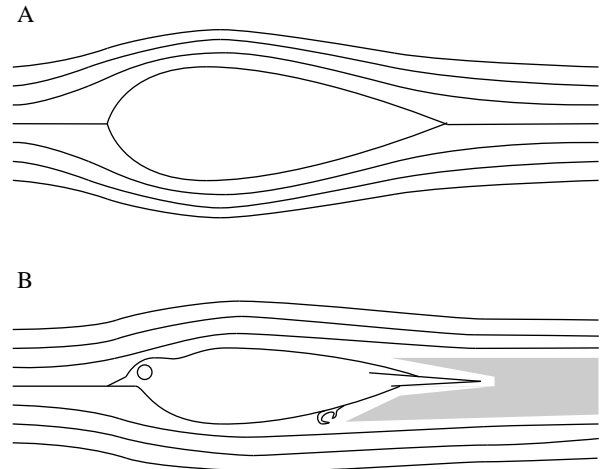

Fig. 7. (A) A streamlined body of revolution with fineness ratio 3. Air streaming from left to right follows stream lines which diverge around the body, but close up again downstream. (B) A frozen bird body with the wings removed, mounted in a wind tunnel. The stream lines do not close up downstream, but leave a wake (stippled) in which the flow is turbulent and the pressure is reduced.

5, to a value near 0.08, would account for our observed values of V_{mp}. This involves rejecting, or at least re-interpreting, a substantial body of published experimental data. We now examine the nature of this evidence and consider whether there could be valid grounds for such a revision.

Anomalous measured body drag coefficients

The drag coefficient expresses the degree to which a body is streamlined, being the ratio of the drag force on the body to that of a theoretical flat plate of the same frontal area (S_b) aligned perpendicular to the air flow. Reviewing measured drag coefficients of frozen bird bodies from which the wings had been removed, Tucker (1990*a*) noted that the results were in line with those expected for 'bluff bodies' and much higher than the values usually observed for 'streamlined bodies'. The meaning of these aeronautical terms is illustrated in Fig. 7. A streamlined body is one in which the stream lines come together smoothly at the downstream end, whereas the stream lines around a bluff body part as the air passes around the body, but fail to come together again downstream. This leaves a 'wake', in which the air pressure is lower than where the air is impinging on the upstream end of the body. The difference in pressure between the upstream and downstream ends is what causes the high drag of bluff bodies. In a perfectly

streamlined body, the pressure would build up along the backward-facing surfaces, to balance that on the upstream end of the body. In that case, the drag would be due entirely to 'skin friction'; that is, to the tangential forces due to the viscosity of the fluid as it slides along the surface of the body. Skin friction depends on the total 'wetted area' of the surface rather than on the frontal cross-sectional area and is therefore increased by such anatomical features as long tails and trailing legs. For bodies of similar shape, skin friction becomes an increasingly prominent proportion of the total drag at smaller scales (smaller size and lower speed). Because of this, drag coefficients, even of well-streamlined shapes, tend to increase at smaller scales, usually expressed by the 'Reynolds number'. An explanation of these effects, with a definition of Reynolds number and related concepts, can be found in Anderson (1991).

The streamlined body of revolution depicted in Fig. 7 has a 'fineness ratio' (length:diameter ratio) of 3. Hoerner (1958), in a classical study of fluid dynamic drag, reported a drag coefficient of 0.015 for a smooth-surfaced body of approximately this shape, decreasing to 0.009 for a fineness ratio of 5. This refers to a Reynolds number of 10^5, which is within the range at which medium-sized bird bodies operate in cruising flight. A drag coefficient of 0.43, as observed for a frozen pigeon body by Pennycuick (1968*a*), is far above the range of values normally measured on streamlined bodies and is nearer the value expected for a sphere. Recognising that this result was anomalous, Tucker (1990*a*) took great care with the technique when measuring the drag of a frozen body of a peregine falcon (*Falco peregrinus*), including a careful investigation of the effect of the mounting strut on the flow over the body itself (further developed by Tucker, 1990*b*). Even after applying downward corrections for all known

sources of error, he obtained a drag coefficient of 0.24 for this apparently well-streamlined species. This is approximately 20 times higher than might be expected from the engineering literature on streamlined bodies. Tucker (1990*a*) also re-examined earlier measurements, applying corrections for shortcomings in technique but, even so, his corrected drag coefficients from published data by Tucker (1973), Pennycuick (1971), Pennycuick *et al.* (1988) and Prior (1984) were all above 0.2. It would seem that frozen, wingless bird bodies behave like bluff bodies when mounted on a drag balance in a wind tunnel. In the absence of evidence to the contrary, it has been assumed that bird bodies behave in the same way in life, but we now question this assumption.

The feather anomaly

The wake in the region of separated flow (stippled in Fig. 7) contains turbulent air, and Pennycuick *et al.* (1988) noted that this turbulence was plainly visible on frozen, feathered bodies, as it caused the feathers to lift and flutter. The measured drag was minimised if the feathers were carefully smoothed down before each observation. In a somewhat bizarre experiment, these authors glued down the feathers of a snow goose body using hair lacquer, having previously measured its drag coefficient (uncorrected for the effect of the mounting struts) as 0.33. After this treatment, the drag coefficient was 0.28, a 15 % reduction. Tucker (1990*a*) went a step further by making a three-dimensional surface survey of his peregrine body and then making an accurate full-sized model out of smooth-surfaced plastic. The drag coefficient of the model was 0.14 compared with 0.24 for the real body, a 42 % reduction. Taken at face value, these results indicate that the feathered surface causes a big increase in drag. If this were really the case, it would be an evolutionary anomaly, as there would seem to be no phylogenetic objection to modifying the outer layer of feathers into smooth, impervious, reptile-like scales.

A streamlined body hypothesis

We propose that the high drag coefficients measured on wingless, frozen bodies are due to extensive separation of the flow, but that this is an artefact that does not occur in the intact bird. Even in small passerines and hummingbirds, the body shape is 'faired' by feathers, which smooth over irregularities caused by the neck and legs, so that the outer surface has the shape of a typical streamlined body, tapering to a point at the posterior end. There would seem to be no advantage in this, unless the apparent streamlined shape actually does guide the air flow so that it remains attached to the surface and joins up downstream to leave a minimal wake. If this does occur, then the engineering literature would lead us to expect drag coefficients of approximately 0.05. Our results (Fig. 5) could be accounted for if the teal and the thrush nightingale both had body drag coefficients of approximately 0.08, rather than near 0.4 as at first assumed. The Reynolds numbers, based on body diameter at the widest point, were 21 600 for the thrush nightingale and 215 000 for the teal. We see no indication that the smaller bird had a higher drag coefficient, although this

was expected, as aeromodellers find it difficult to keep the flow attached to streamlined bodies at the low Reynolds numbers seen in small birds. This result suggests that, far from promoting separation as observed in the measurements on frozen bodies, the feathered surface, on the contrary, helps to keep the flow attached to the surface. We note that insects, which do not have any equivalent of the feathered surface, do not have streamlined shapes either, indicating that, at their lower Reynolds numbers, separated flow is inevitable and cannot be prevented by streamlining.

Aerodynamic cleanness

The thrush nightingale flew with its tarsal joints flexed and its feet forward. The legs and feet could be completely concealed under the feathers, giving the outer body surface a smoothly streamlined shape, although sometimes the toes could be seen projecting from the feathers. The teal held its feet just below the tail when flying in the wind tunnel, where they would be expected to create a small amount of drag. Birds' feet are extremely effective at creating additional drag when stretched out with the toes spread (Pennycuick, 1971). A bird's body may be said to be aerodynamically 'clean' when all irregularities that might cause flow separation, such as the head, neck and feet, are retracted and faired smoothly into a streamlined shape by an outer layer of feathers. Both the teal and the thrush nightingale might possibly be capable of fairing over their feet more completely than they actually did and, in that case, the drag coefficients that we estimated (near 0.08 for both birds) might not be the minimum of which they are capable. The best interpretation that we can place on our results is that birds whose bodies have well-streamlined shapes, as in the teal and thrush nightingale, are capable of minimum drag coefficients, when fully 'cleaned up' aerodynamically, in the region of 0.05. However, it is possible that much higher drag coefficients, characteristic of bluff bodies rather than streamlined bodies, may actually occur in species with aerodynamically 'dirty' body shapes, such as pelicans and large herons, with their prominent heads and long, trailing legs. Irregularities of outline may be expected to promote flow separation, while features that increase the wetted area will increase skin friction. All birds can increase their body drag when required, as in steep descents, by lowering and spreading their feet, except possibly for a few species with very small feet (swifts, frigatebirds).

Implications of lower drag coefficients

Our hypothesis, which remains to be tested by future experiments, is that the flow around living bird bodies (as opposed to frozen, wingless bodies) remains attached to the surface, giving a 'streamlined' rather than a 'bluff body' type of flow, with drag coefficients far lower than have been generally assumed. If this is correct, then the default values for body drag coefficient used in the computer programs of Pennycuick (1989) will in most cases be too high. Our results suggest that a default value of 0.05 should be used for the body drag coefficient of any well-streamlined species that is capable
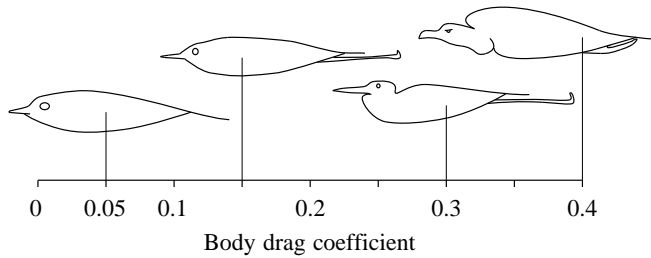
Fig. 8. Suggested values for the body drag coefficient C_{Db} for use in computer programs such as those of Pennycuick (1989) for calculating flight performance. C_{Db} may be as low as 0.05 in species whose heads and feet can be fully faired by feathers. At the other extreme, species with prominent heads and long legs may behave like 'bluff bodies' with drag coefficients as high as 0.4. These suggestions are provisional, pending actual measurements.

of completely retracting its feet, irrespective of size. This replaces the old default values of between 0.25 and 0.40 which are computed in the published version of the programs. In the case of species with long legs, large feet or prominent heads, higher drag coefficients may be appropriate, intermediate between the old and new default values. Fig. 8 represents this in a graphical way and should be regarded as a provisional suggestion, pending better measurements on species with different body shapes.

A drastic downward revision of the default body drag coefficient will have two practical consequences. (1) The minimum power speed will be revised upwards, by an amount similar to that seen in Fig. 5. This may cause some surprises when field data on flight speeds are re-examined. Birds which appeared to be flying at their maximum range speeds under the old assumptions may turn out to be flying nearer their minimum power speeds. Some birds may appear to fly even slower than their minimum power speeds, which may be due to aerodynamically 'dirty' body shapes, with drag coefficients between the old default values and the revised values. (2) The power in cruising flight will be less than previously estimated and the effective lift:drag ratio will be greater. The distance that a bird can fly with a given fraction of its take-off mass as consumable fuel (its 'range') depends directly on the effective lift:drag ratio and will be increased in the same proportion.

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